

## DISCUSSION

D. R. Bellwood

**What are reef fishes? - Comment on the report by D. R. Robertson:  
Do coral-reef fish faunas have a distinctive taxonomic structure?  
(*Coral Reefs* 17: 179–186)**

Accepted: 24 November 1997

What are reef fishes? This is a simple question, yet the answer remains elusive. Robertson (1998) in commenting on a series of studies by Bellwood and Choat has added to the debate. The designation 'reef fishes' is widely used by researchers working on coral reefs, with numerous books and papers referring to 'coral reef fishes'. However, the criteria used in identifying those taxa or individuals that constitute 'reef fishes' are rarely defined. To address this problem, Bellwood (1996) established a 'consensus list' of fish families as a working definition of a reef fish assemblage. This list contained fish families that would be found on any living coral reef, irrespective of its biogeographic location, i.e. the essence of a modern reef fish fauna. Being based solely on taxonomy, it permitted direct comparisons between widely separated biogeographic areas and fossil deposits. Using this list, Bellwood (1996) concluded that the Eocene fossil fish assemblage in Monte Bolca contained a significant reef fish component. Subsequently two studies have re-examined the utility of the 'consensus' list and its implications for the fishes of Monte Bolca.

Robertson (1998) questioned the view that reef fish have distinguishing taxonomic characteristics and that the Bolca fauna was a reef fish assemblage based on a study of four sites in the Caribbean and the central/eastern Pacific. At the same time, Bellwood (1997) examined the faunal composition of fish assemblages at 24 widespread reef and non-reef sites. Both workers concluded that the consensus list provides a description, not a definition, of a reef fish assemblage.

Bellwood (1997) found that fish faunas on coral reefs were characterised by high species richness in 'consen-

sus list' families. However, the consensus list definition could not separate the Great Barrier Reef from Ascension Island (a rocky island with few, if any, corals; Lubbock 1980). Indeed, many of the consensus list families were among the 10 most speciose families in New Zealand, an area devoid of coral reefs. The consensus list appears to define a shallow tropical/subtropical benthic fish fauna, from an area with topographic complexity. In many locations this equates to coral reefs. However, it may equally well include a range of non-reef habitats. The consensus list therefore, is descriptive, not diagnostic. Whilst some definition of a reef fish fauna may be possible based on patterns of diversity and abundance (see Dunfren and Legendre 1997), there appears to be no strong taxonomic division, at the family level, between many reef and non-reef fish faunas. As noted in Bellwood (1996) 'reef fish' families are characteristic of, but not restricted to, coral reefs.

Ecology is unlikely to provide a better definition than taxonomy. Although several studies have evaluated the status of coral reefs in terms of the ecological attributes of the component taxa (Bellwood 1988; Choat and Bellwood 1991; Landini and Sorbini 1996) none provide a diagnostic definition. Ecological categories are unlikely to be diagnostic given the broad trophic and taxonomic overlap between reef and non-reef assemblages. If the critical aspect of a reef fish is its interaction with the coral reef per se, then the definition of reef fishes may be trivial and tautological: reef fishes are those individual fishes that live on coral reefs.

Robertson (1998) compared the total species richness and relative species richness of consensus list families at a pair of sites in French Polynesia and between sites in the East Pacific and West Atlantic. Although the findings are consistent with those of Bellwood (1997), Robertson's analyses are compromised by the limited number of sites examined and the

D. R. Bellwood  
Department of Marine Biology, James Cook University, Townsville  
Q4811, Australia e-mail: David.Bellwood@jcu.edu.au

effects of historical biogeography and regional current patterns. Bellwood (1996) claimed that most consensus list families reach their greatest diversity on reefs. This cannot be disproved by analyses of two reef sites both of which are at the lower end of the range of species richness recorded from coral reefs. Furthermore, Robertson used data from two pairs of sites: (1) the Marquesas (non-reef) and French Polynesia (reef) and (2) the North Western Atlantic (reef) and the East Pacific (non-reef). In the first pair, the two sites are in close juxtaposition and species compositions may be strongly influenced by their location i.e. at the outermost edge of the Central Pacific reef zone. Furthermore, as the Marquesas are downcurrent from reefs to the west there is a strong possibility of larval input to the Marquesas and the maintenance of local non-reproductive populations. Whilst endemics indicate that some local populations are maintained in the Marquesas, larval input may be important when looking at total species richness.

In the second pair of sites, the Tropical E Pacific (non-reef) has low coral cover but it lies in the relatively species-rich Indo-Pacific realm, with links to 'reef fish' families in the Central Pacific (see Rosenblatt and Waples 1986). In contrast, the reefal site (NE tropical Atlantic) is in the relatively depauperate Atlantic reef system. Thus, the two pairs of sites are either closely linked low diversity systems or from different biogeographic zones, comparing a low-diversity reef system with a rocky reef assemblage in a high-diversity system. In both cases, the situation is likely to increase the chances of finding no difference in the composition of the respective faunas.

A critical evaluation of the composition of reef fish faunas may benefit from an analysis of a broad range of benthic habitats, including the high-diversity reefs in the West Pacific and adjacent non-reef areas. To date, the debate has been limited by restricted sampling and the use of different criteria to identify reef fishes. At this time, it may be more instructive to concentrate less on the definition of a reef fish fauna, and more on identifying the role of history and habitat associations in shaping the fish faunas found on modern coral reefs.

---

#### **What is the status of the fishes of Monte Bolca?**

If living fish faunas on coral reefs cannot be distinguished from those in other tropical marine habitats, it may be difficult to determine the habitat associations of the Bolca fishes. The Bolca fishes are perhaps most accurately viewed as a coastal tropical fish fauna containing both benthic and open-water forms. The benthic substratum may have been reefal but there is little direct evidence of a coral reef.

Despite the uncertainty over the status of the Bolca fishes as 'reef fishes' their importance is undiminished. The Bolca fish deposits clearly establish that:

1. Perciform fishes were well established in Eocene tropical marine waters and were probably the dominant benthic fish group.
2. The fish families which dominate all of the world's coral reefs today, both numerically and in species richness, were present in one region of the central Tethys 50 Ma ago.
3. These fish were morphologically similar to modern forms.

Whether these fish lived and fed on coral reefs remains open to question. It is quite possible that early 'reef fish' assemblages lived without coral reefs. Today there are few, if any, fish families that are obligate coral reef dwellers. Furthermore, based on phylogenetic analyses, Bellwood (1997) suggested that many 'reef fish' lineages may have evolved in non-reef environments before moving onto coral reefs, e.g. acanthuroids from coastal soft sediments and scarids from seagrasses.

Unfortunately, the Bolca fish deposits are out of context, i.e. the facies have been displaced. But even if a reef was preserved in close juxtaposition, evidence of an interaction, the ecological essence of a modern reef fish, would still be lacking. In a recent reappraisal of the Bolca (Pesciara) deposits, Landini and Sorbini (1996) emphasised the lack of clear trophic links with a coral reef, although they suggested that the sediments in which the fish were fossilized were delineated by a coral reef. Their palaeoenvironmental reconstruction reveals a tropical coastline with fluvial influences and coastal lagoons, and vast areas of *Halochloris* sand and/or seagrass. The site is regarded as perireefal. The presence of adjacent coral reefs is inferred from the periodic deposition of reef bioclasts in the sedimentation basin.

The fish probably died of asphyxia relatively close to the site of deposition, as most are preserved with an open gape but with no evidence of abrasion, visceral distension or fin damage during transportation. The fishes are preserved in finely laminated limestones indicative of calm waters (probably several tens of meters deep). The lack of bioturbation, limited number of benthic invertebrates, no scavenging, excellent preservation and widespread presence of pyrite and bitumen (Massari and Sorbini, 1975), are all indicative of chronic anoxia in the waters immediately above the sediments. However, coprolites in the deposits suggest that oxygenated waters overlaid these deeper anoxic layers. The inclusion of large fish (over 1.0 m) and oceanic forms (including a larval acanthurid) suggest that the periodic asphyxiating events covered a considerable area, including the adjacent open water. Outflows of toxic water from algal blooms in enclosed lagoons, escaping volcanic gasses, or periodic

upwelling of the deeper anoxic waters would all produce the observed mortalities.

We may never know the identity of the fishes that lived on ancient coral reefs. Although the Bolca fish were apparently preserved in the vicinity of a reefal structure (see Massari and Sorbini 1975; Landini and Sorbini 1996), there is no direct evidence of faunal links with a reef. Nevertheless, the Bolca deposits lie in the central Tethys, a region that had seen extensive coral growth since the Oligocene. The fish families from the Bolca deposits are morphologically, and probably functionally, analogous to modern taxa. Given the lack of habitat specificity in these families today, it appears highly likely that some of these fishes would have lived on coral reefs but, as today, this may have been a facultative relationship. Coral reefs probably represented *a* habitat, not *the* habitat for these families.

In conclusion, it appears that at present 'reef fishes' defy definition beyond the tautological: reef fishes are those individuals that live on coral reefs. Likewise, in examining the history of fish families found on coral reefs, it must be noted that coral reefs represent only one of a number of habitats with which these families have been associated. The resolution to this problem may be best exemplified by Sale (1991) who in compiling a book on the 'ecology of reef fish' (sic.) prophetically entitled it not 'The ecology of reef fishes' but 'The ecology of FISHES ON CORAL REEFS'.

**Acknowledgements** I wish to thank JH Choat for comments on the manuscript, DR Robertson for lively discussions, and PF Sale for valuable editorial guidance. Finally I wish to thank the late Dr. Lorenzo Sorbini for introducing me to the fishes of Monte Bolca. He will be sorely missed.

## References

- Bellwood DR (1988) Seasonal changes in the size and composition of the fish yield from the reefs around Apo Island, Central Philippines, with notes on methods of yield estimation. *J Fish Biol* 32: 881–893
- Bellwood DR (1996) The Eocene fishes of Monte Bolca: the earliest coral reef fish assemblage *Coral Reefs* 15: 11–19
- Bellwood DR (1997) Reef fish biogeography: habitat associations, fossils and phylogenies. *Proc 8th Int Coral Reef Symp*, Panama 1: 379–384
- Choat JH, Bellwood DR (1991) Reef fishes; their history and evolution. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic Press, London, pp 39–66
- Dunfren M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecol Monogr* 67: 345–366
- Landini W, Sorbini L (1996) Ecological and trophic relationships of Eocene Monte Bolca (Pesciara) fish fauna. In: Cherchi A (ed) *Autecology of selected fossil organisms: achievements and problems*. Boll Soc Paleont Ital Spec 3, Mucchi, Modena, pp 105–112
- Lubbock R (1980) The shorefishes of Ascension Island. *J Fish Biol* 17: 283–303
- Massari F, Sorbini L (1975) Aspects sedimentologiques des chouches a Poissons de l' Eocene de Bolca (Verone-Nord Italie). IX Congres International de Sedimentologie, Nice: 55–61
- Sale PF (1991) (ed) *The ecology of fishes on coral reefs*. Academic Press, London, 754 pp
- Robertson DR (1998) Do coral-reef fish faunas have a distinctive taxonomic structure? *Coral Reefs* 17: 179–186
- Rosenblatt RH, Waples RS (1986) A genetic comparison of allopatric populations of shore fish species from the Eastern and Central Pacific Ocean: dispersal or vicariance? *Copeia* 1986: 275–284